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The interaction of brain regions during visual search processing as revealed by transcranial magnetic stimulation.

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Abstract

Although it has long been known that right posterior parietal cortex (PPC) has a role in certain visual search tasks, and human motion area V5 is involved in processing tasks requiring attention to motion, little is known about how these areas may interact during the processing of a task requiring the speciality of each. Using transcranial magnetic stimulation (TMS), this study first established the specialisation of each area in the form of a double dissociation; TMS to right PPC disrupted processing of a colour/form conjunction and TMS to V5 disrupted processing of a motion/form conjunction. The key finding of this study is however, if TMS is used to disrupt processing of V5 at its critical time of activation during the motion/form conjunction task, concurrent disruption of right PPC now has a significant effect, where TMS at PPC alone does not. Our findings challenge the conventional interpretation of the role of right PPC in conjunction search and spatial attention.

Keywords: attention; conjunction search; motion processing; posterior parietal cortex; TMS; V5.

Introduction

Transcranial magnetic stimulation (TMS) has been successfully used to identify areas in the brain which are critical for given behavioural tasks. However, most behavioural tasks involve not just one brain area but a whole network of them, each area with its own functionality in the processing of the task. Functional imaging has helped us to identify the networks of relevant areas, but does not determine how they interact.

In our study, we employ a dual-site TMS approach to study the interaction of two areas which have both been implicated in different aspects of visual search. In recent years, the visual search task has been used as a tool to answer questions about neural processing in the human brain. Taken together, various neuropsychological, neuroimaging and TMS studies seem to suggest that PPC is involved in spatial search for conjunction items irrespective of search difficulty (Friedman-Hill, 1995, Corbetta & Shulman, 1998; Shafritz *et al.*, 2002; Nobre *et al.*, 2003; Ellison *et al.*, 2003). It is also known that V5 has a vital role to play in the processing of visual search tasks in which attention to motion is required (McLeod *et al.*, 1989; Walsh *et al.*, 1998).

The exact contribution of V5 to motion processing in these tasks may lie in its known properties as a motion filter (McLeod *et al.*, 1989, 1991). While the perception of movement per se and the identification of the movement direction of individual objects does not require V5 (Andersen *et al.*, 1990), V5 is critically involved in the integration of movement across multiple visual items (e.g. Newsome & Paré, 1988). The role of V5 for this so-called global motion perception has been demonstrated using single-unit recordings (Born & Tootell, 1992), lesion studies in monkeys (Newsome & Paré, 1988) and humans (Baker *et al.*, 1991; Schenk & Zihl, 1997),

transcranial magnetic stimulation (Beckers & Homberg, 1992) and functional imaging (Culham *et al.*, 2001). V5 is required to group objects of similar motion properties together which conversely allows the segregation of groups of objects with different motion properties. This is for example illustrated by its involvement in form-from-motion tasks (Rizzo *et al.*, 1995). In a motion/orientation conjunction search task, V5 can help to separate the moving items and the non-moving items into different groups, so that the subsequent search can be focussed on the moving items. Consequently, within the group of moving items the target is clearly identified by its unique orientation, making the search for the target significantly easier. This scenario is supported by the fact that the search rate for motion/orientation conjunction is smaller than that for other types of conjunction tasks (e.g. McLeod *et al.*, 1989). Selective disruption of V5 will still allow the detection of motion, since many other areas in the visual cortex respond to visual motion as well, but it will impair the grouping of objects with shared motion properties, and therefore make the search for targets which are defined by a combination of motion and form more difficult. This was in fact confirmed by a study with the V5-lesioned patient LM. In contrast to healthy subjects LM's search for a motion-conjunction target was not more efficient than that for other conjunction targets (McLeod *et al.*, 1989).

The first question of the current study is concerned with establishing whether it is only V5 which is vital for such a motion/orientation task or whether PPC (which is accepted to be involved in conjunction search) is also required. However, a more important question relates to how the brain responds to the disruption of V5. Given that in this case, the motion filter can no longer be used to isolate moving items into a coherent group of common fate, the task should now be treated as a normal

conjunction search, and PPC may again become important for its processing. This would be reflected by an increase in reaction time when both V5 and PPC are stimulated which is in addition to the increase observed for V5 stimulation alone or for stimulation of V5 in combination with a control site (such as vertex).

Materials and Methods

Subjects

Seven healthy subjects, aged 18-31, with normal or corrected to normal vision (all right handed; five female, two male), participated in all tasks. Subjects gave their signed informed consent in accordance with the Declaration of Helsinki and with the approval of Durham University Ethics Advisory Committee, and could leave the experiment at any point. Subject selection complied with current guidelines for repetitive TMS research (Wassermann 1998).

Stimuli

All stimuli were presented on a 320mm x 240mm monitor driven by a Pentium-4 PC programmed in E-Prime (Psychology Software Tools, Inc). Subjects were seated comfortably 57.5 cm away from the screen with the centre of the screen at pupil level. The subjects' head and trunk sagittal midline was aligned with the centre of the screen, and head position was controlled by a chinrest. Except for the light from the PC screen the room was darkened.

Visual Search Tasks

Two visual search tasks were used (see Figure 1). In both tasks, all items subtended $1^\circ \times 1^\circ$ visual angle and were presented against a black background. Subjects were asked to respond as quickly and as accurately as possible on a button box (left button for target-present, right button for target-absent) to indicate the presence or absence of the target. Each trial was preceded by a central fixation cross ($0.5^\circ \times 0.5^\circ$) for 500ms followed immediately by the stimulus array. There were 8 distractor items in each array, 4 of each distractor set. In trials where the target was absent, an extra distractor was displayed to eliminate counting as a strategy. The target was present in 50% of trials, and there was never more than one target. The visual array remained present until response or for 2000ms, whichever was shorter, and the inter-trial interval was 4000ms.

The colour/orientation conjunction task required search for a red slash (/) target amongst red backslashes (\) and green slashes. In the motion/orientation conjunction task the target was a moving red slash with moving red backslashes and stationary red slashes as distractors. Movement was constant at 21° s^{-1} and moving items were allowed to scroll from the bottom to the top of the screen. The movement of items was never impeded by stationary objects (see Figure 1).

Figure 1 about here please.

TMS

A Magstim™ Model 200 was used to apply 5 pulses 100ms from visual stimulus onset (10Hz) at 65% of the stimulator's maximum power (*i.e.* 1.3 Tesla). A

Magstim™ BiPulse machine was also used to apply double pulses of TMS at 65% of the stimulator's maximum power 50ms apart. This intensity of stimulation was chosen as it is super-threshold to both areas of cortex investigated (see Stewart *et al.* 2001, for details).

Two sites of stimulation were used right posterior parietal cortex, PPC and the visual motion area V5. The PPC site was identified by using a hunting procedure with the hard conjunction task, as described in Ashbridge *et al.* (1997) and employed by Ellison *et al.*, (2003). In the hunting procedure, 10 trials of TMS are given to each site in a 3 x 3 grid around a central point 9 cm dorsal to the mastoid-inion and 6cm lateral. The “hotspot” for activation is denoted by a 100ms increase in reaction time over the trials in which no TMS was administered. This functionally localised position was then verified using BrainSight™ (Rogue Research, Montreal, Canada) (see Figure 2). A 70mm figure-of-eight coil placed tangential to the skull with the handle of the coil parallel to the mid-sagittal plane pointing in anterior direction was used to stimulate right PPC. This was done to accommodate a second coil positioned at right V5 in the dual-site experiment but this orientation was used throughout all experiments.

Figure 2 about here please

Right V5 (generally corresponding to 3cm above the mastoid-inion and 5cm lateral to the right) was found by localising the area where a train of 5 TMS pulses (10Hz) elicited the strongest and most salient moving phosphenes (see Schenk *et al.*, 2005) at the lowest TMS intensity. This was further localised using the hunting procedure (the central point being that which elicited the strongest moving phosphenes) with the

motion/orientation conjunction task. Using BrainSight™, this was verified to be at the widely accepted anatomical location for V5 (see Figure 2). A 50mm figure-of-eight coil placed tangential to the skull was used to stimulate this more focal area of cortex. The smaller coil was also used at this site to allow space on the skull for two coils. As the small coil is in the form of a branding iron, the handle direction is perpendicular to the skull. In all subjects however, the coil windings were positioned such that current flowed in an anterior-posterior direction. The same coil orientation was used throughout the experiments. When both coils were used concurrently, the foci of stimulation were on average 6cm apart on the skull.

Experiment 1

The purpose of this experiment was to determine the search rate for the two visual search tasks. Subjects were asked to complete 60 trials without TMS in which the number of distractors, and thus the set-size was varied (4, 8, 16). This was done for both the colour/orientation and motion/orientation conjunction tasks. The search rate, i.e. the slope of the search function was calculated by using the conventional formula for computing the slope of a linear function, namely $(x_2 - x_1) / (y_2 - y_1)$.

Experiment 2

The purpose of this experiment was to determine the involvement of the right PPC and the right V5 in the two visual search tasks using rTMS. Subjects were stimulated at either the right PPC or V5 site for four blocks of 24 moving/form conjunction trials and four blocks of 24 colour/form conjunction trials. TMS stimulation started at the onset of the presentation of the search array. In Experiment 2 (and in all following experiments) the set-size was limited to 8 items. A sham stimulation was used in four

blocks in each task. In the sham condition a non-discharging coil was placed over the area of interest while a discharging coil was placed in close proximity to the subject. The subjective experience of the noise associated with a TMS pulse was therefore the same as was the tactile experience of a coil placed on the head, however no pulse was administered into the brain. Half of the subjects experienced the V5-stimulation during the first session, and the PPC-stimulation during the second session. This order was reversed for the other half of the subjects. In both sessions sham-stimulation was intermingled with the V5 or PPC stimulation. In session two, the same blocks of trials were completed with stimulation occurring at the other site of interest.

Sessions one and two therefore had 16 blocks each in which block and site order were randomised across subjects to minimise either order or practice effects.

Experiment 3

This experiment was necessary to determine the correct parameters for Experiment 4. In Experiment 4 (see below) we wanted to examine the effect of combining TMS over V5 and PPC. Since our equipment only allowed us to combine dual pulse TMS over one site with rTMS at a different site, we first needed to establish the best time period for delivering a double-pulse over V5 (dTMS, two pulses 50 ms apart). To do this we examined search performance in the motion/orientation task using five different time intervals during which dTMS (0/50, 50/100, 100/150, 150/200, 200/250 ms after the onset of the search array) was delivered, and selected those intervals which resulted in a significant increase in search time. TMS was applied in 6 blocks of 40 trials interspersed by 6 blocks of 40 trials with sham TMS to control for practice effects.

This provided data from 48 trials in each TMS time bin. Again, block order was randomised across subjects.

Experiment 4

The purpose of this last experiment was to examine the effect of a combined stimulation of both V5 and PPC on search performance in a motion/orientation task. In session four, TMS was applied over V5 at three different time intervals measured from the onset of the presentation of the search array, namely 100+150, 150+200, 200+250. This selection of time-intervals was based on the results from Experiment 3. Only intervals during which V5-stimulation on its own yielded a significant performance disruption in the motion/orientation task were included. In addition a pulse train of 10Hz for 500ms was applied to right PPC at the onset of the search array for 6 blocks of 24 trials. These blocks were interspersed with three blocks of 24 trials in which V5-stimulation was combined with vertex stimulation (anatomical centre of the skull) and three blocks of 24 trials with sham-TMS. For the V5 stimulation we used the same parameters as before (i.e. double-pulse at three time intervals). For the vertex stimulation we used the same stimulation parameters as for PPC.

In total each subject participated in four 1.5 hour testing sessions. Sessions were each one week apart.

Statistical Analysis

Mean reaction times were compared using repeated measures general linear models to test for TMS effects. The normalised TMS effect was also computed for each subject

by using the following formula: $(\text{TMS reaction time} - \text{sham TMS reaction time}) / \text{sham TMS reaction time} \times 100$. These effects were compared using repeated measures general linear models. Significant results were further investigated using pair-wise post-hoc tests with corrections for multiple comparisons. In experiment 4, TMS effects for each time interval of stimulation were investigated using two-tailed one sample t-tests with corrections for multiple comparisons.

Results

In all experiments, error rates were less than 4% and for clarity, only reaction times for target-present responses were analysed.

Experiment 1: The search functions and search rates for both search tasks are presented in Figure 3a. For both tasks a serial search function was obtained, however the motion/orientation conjunction search was more efficient than the colour/orientation conjunction. (i.e. search rate for colour/orientation task: 35.86 ms per item [sd: 7.22 ms/item]; search rate for motion/orientation: 21.72 ms per item [sd: 5.11 ms/item]).

Experiment 2: In this experiment we examined the effect of rTMS either over PPC or V5 on performance in both search tasks. The results are presented in Figure 3b. A three factor (*site* [PPC v V5] x *task* [colour/form conjunction v motion/form conjunction] x *TMS* [TMS v sham TMS] repeated measures general liner model (GLM) revealed a significant main effect for TMS ($F_{(1, 6)} = 10.586$, $p = 0.017$) and a

significant interaction between site, task and TMS ($F_{(1, 6)} = 31.806$, $p = 0.001$). A two factor (*task x site*) repeated measures GLM carried out on the normalised TMS effect at each site for each task revealed a significant interaction between task and site ($F_{(1, 6)} = 30.936$, $p = 0.001$). Post-hoc Bonferroni tests show that the source of these interactions lies in the significant effect of TMS over right PPC in the colour/orientation conjunction task ($t = -3.435$, $df = 6$, $p = 0.014$) but not the motion/orientation task ($t = -1.204$, $df = 6$, $p = 0.274$), and the significant effect of TMS over V5 in the motion/orientation conjunction task ($t = -5.538$, $df = 6$, $p = 0.001$) but not the colour/orientation conjunction task ($t = -0.261$, $df = 6$, $p = 0.803$) (see Figure 3b). There was no significant difference between the TMS effect seen at right PPC for the colour/orientation conjunction and V5 for the motion/orientation conjunction task. In a separate analysis we examined whether there were differences in the TMS effect between the right and left visual hemispace for the two search tasks. However, we did not find significant hemispace differences for either V5 or for PPC (see Table 1).

Figure 3 and Table 1 about here please.

Experiment 3: In this experiment we identified the critical time period for delivering a dTMS pulse over V5. Two-tailed one sample t-tests (alpha level corrected for multiple comparisons = 0.01) on the normalised TMS effect at each time bin (comparison value: 0) showed that TMS had a significant effect at the 100/150 ms ($t = 6.474$, $df = 6$, $p = 0.001$), 150/200 ms ($t = 4.094$, $df = 6$, $p = 0.006$) and 200/250 ms ($t = 6.374$, $df = 6$, $p = 0.001$) onset asynchronies. Therefore we used these three onset asynchronies in Experiment 4. The results are presented in Figure 4.

Figure 4 about here please.

Experiment 4: In this experiment the combined effect of V5 and PPC stimulation on search performance in the motion/orientation task was examined. Reaction times from each of the three time periods used in V5/MT TMS were not significantly different from each other and so were pooled in the analysis of Experiment 4. When a 5 pulse train (10Hz) of TMS was applied to right PPC while V5 was disrupted at the critical times found in Experiment 1, reaction times were significantly slower than when V5 was stimulated alone or when a pulse train was delivered to vertex concurrently with double pulses to V5 (see Figure 5).

Figure 5 about here please.

A one factor (site [V5, V5 + vertex, V5 + PPC]) repeated measures GLM revealed a significant main effect of TMS across sites ($F_{(2, 40)} = 12.589, p = 0.000$).

Post-hoc Bonferroni tests show that there was a significant increase in reaction time when right PPC was stimulated with V5 over that seen when V5 is stimulated alone ($t = -4.695, df = 20, p = 0.000$). There was also a significant difference between reaction times when PPC was stimulated with V5 and when vertex was stimulated with V5 ($t = -3.080, df = 20, p = 0.006$) indicating that this effect is not one mediated by a general factor such as dual-site stimulation. To corroborate this point, there was no significant difference between reaction times when V5 was stimulated with vertex and when V5 was stimulated alone ($t = -1.205, df = 20, p = 0.242$). A separate paired sample t-test

was carried out to demonstrate a significant difference between the effect of TMS at V5+PPC and that seen when PPC was stimulated alone ($t = 3.331$, $df = 6$, $p = 0.016$). Again, we examined whether the TMS effect was different for the right versus the left visual hemispace. However, we did not find significant hemispace differences for any of the stimulation conditions. (see Table 1).

Discussion

We tested the interaction of areas V5 and PPC in a visual search task by using dual-site TMS stimulation. It is well known that both areas are involved in visual search tasks. It is however not known whether and how they may interact during a task in which each may be theoretically involved. Using a motion/orientation conjunction search, we found evidence of an interaction between the two areas. V5 disruption appears to act as a gate for PPC involvement, i.e. PPC stimulation affects search performance in a motion/orientation task only when it is applied in combination with V5-stimulation. Importantly, this gating effect seems to be specific to V5, if stimulation of PPC is combined with stimulation of vertex, no significant TMS effect is observed. In the following we will discuss possible explanations for this interaction and explore the implications of these findings for our understanding of the role of PPC in visual search tasks and in the control of spatial attention.

One explanation for this interaction can be derived from the motion-filter hypothesis which we described in the Introduction. According to this hypothesis V5 acts as a motion-filter, it allows for the grouping of all moving stimuli and thereby facilitates the segregation of moving from stationary stimuli. Once this separation is achieved, the search can be restricted to the group of moving stimuli. Within that group the target is clearly defined on the basis of a single feature, in our case its orientation. The motion-filter transforms a motion/orientation conjunction search into a simpler orientation search as indicated by the flatter search function. It is thus expected that while the motion-filter is intact, feature-binding is not required. PPC which is primarily concerned with feature-binding will, therefore, not be involved. However, once the motion-filter is impaired, moving and stationary stimuli are no longer

separated, the target has to be searched among both the stationary and the moving stimuli and that its detection requires the identification of two features (i.e. orientation and motion). This requires feature-binding, and therefore also involves the PPC. This explanation fits very well with our own findings but also with previous findings relating to the functional role of PPC and V5. Firstly, we have shown that in the absence of V5-stimulation (i.e., while the putative motion-filter is intact) PPC is not involved in motion/orientation search. Secondly, we found that when V5 is disrupted, a significant PPC-stimulation effect is observed, suggesting that PPC now becomes crucially involved in the motion/orientation search task. However, it also fits with previous characterization of PPC as an area crucially involved in feature-binding (e.g. Ashbridge *et al.*, 1997; Ellison *et al.*, 2003, 2004) and with previous findings showing that V5-disruption does not abolish the perception of motion, but selectively impairs the grouping of moving stimuli and the perception of motion coherence (e.g. Beckers & Homberg, 1992, Cowey *et al.*, 2006).

However, this is not the only possible explanation for the observed interaction between V5 and PPC stimulation. It is also possible that cross-hemispheric effects of the unilateral stimulation account for the increased response delay which we observed when we combined V5 and PPC stimulation. In this context it is important to note that our TMS stimulation was restricted to the right hemisphere. However, this does not necessarily mean that the effects of this stimulation were restricted to just this hemisphere. In fact we know from clinical (Corbetta *et al.*, 2005) but also rTMS studies that disruption of an area in one hemisphere can lead to changes in the activity of homologue areas in the other hemisphere (Bonato *et al.*, 2006; Komssi *et al.*, 2002). Moreover, in the case of neglect, it was demonstrated that TMS stimulation of

the “unaffected” hemisphere can alleviate the symptoms caused by the real or virtual lesion in the opposite hemisphere (Hilgetag *et al.*, 2001; Brighina *et al.*, 2003). One might therefore suggest that the reason why the effect of PPC stimulation is more pronounced when V5 is stimulated at the same time is not that the areas are functionally interlinked, but that their combined stimulation exerts a more potent effect on the activity of contralateral PPC. This would suggest that stimulation over right-hemispheric V5 somehow adds to the effect that stimulation of right-hemispheric PPC has on the activity of left-hemispheric PPC. This assumption is problematic given that cross-hemispheric effects have been primarily demonstrated between homologue areas (e.g. Bonato *et al.*, 2006; Komssi *et al.*, 2002). It is also important to note that the technique used to induce cross-hemispheric effects was 1Hz long-term rTMS. It is currently unclear whether the methods used in our study, namely 10 Hz short-term rTMS, yields similar functional effects. In summary, while the possibility of cross-hemispheric effects cannot be excluded, the motion-filter hypothesis seems to provide a better fit to the available data.

Our findings also have implication with regards to the role of PPC in visual search. It has long been assumed that PPC is primarily involved in the feature-binding aspect. In line with Treisman’s classical distinction between conjunction and feature search, it is therefore expected that PPC is involved in conjunction but not in feature search (Friedman-Hill, 1995, Corbetta & Shulman, 1998; Shafritz *et al.*, 2002; Nobre *et al.*, 2003). This was in fact confirmed in rTMS studies (Ashbridge *et al.*, 1997; Ellison *et al.*, 2003), however, our current findings suggest that there are exceptions. In the case of the motion/orientation task no effect of PPC-stimulation was found. Does this mean that PPC is not involved in feature-binding? We think that PPC is involved in feature-

binding, but our conjunction task does not require the binding of features. There are two possible reasons why a motion/orientation conjunction task does not invoke PPC conjunction processing. The first explanation relates to the motion-filter hypothesis which was described above and suggests that the motion-filter effectively turns the conjunction search into a feature search. The second explanation relates to the physiology of cells in V5. These cells combine orientation and motion-selectivity (Van Essen, 1985). This means that the two features which are relevant for the search are already combined at the level of the individual neuron and, therefore, additional feature-binding is not required. Currently it is not possible to decide between these two explanations.

These results also have ramifications for the role of spatial attention in visual search tasks. It is commonly assumed that serial search rates indicate that the task requires spatial attention (Treisman & Gelade, 1980; Woodman & Luck, 2003; Nobre *et al.*, 2003). Moreover, it is also accepted that the right PPC is critical for the deployment of spatial attention (Corbetta & Shulman, 1998; Nobre *et al.*, 2003; Ashbridge *et al.*, 1997; Ellison *et al.*, 2004). However, our findings are at odds with these two assumptions. The motion/orientation task used in our study yielded a serial search function, but it appeared that PPC was not critically involved in this task. This suggests that at least one of the two assumptions is incorrect: either serial search functions do not necessarily indicate the involvement of spatial attention, or the effective control of spatial attention does not critically depend on PPC.

In conclusion, our findings suggest that if the interaction of different visual areas is taken into account, some of the well-established associations between aspects of

visual search and their underlying neural mechanisms are challenged. For example our results suggest that conjunction search does not always require feature-binding, and therefore does not always involve the PPC. They also suggest that if serial search is taken as an indicator of the involvement of spatial attention, PPC is not always involved when spatial attention is required. This study illustrates how dual-site TMS can go beyond the identification of crucial brain areas and help to uncover the interaction and the specific roles of different areas within a functional network.

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Figure Legends:

Figure 1: Experimental design. Two visual search tasks were used, a colour/orientation and a motion/orientation conjunction task. The targets were a red, stationary slash (solid /) and a downward moving slash (/) respectively. The array was preceded by a fixation point visible for 500ms. TMS was applied in either double pulse or repetitive pulse form in the 500ms interval post stimulus array onset.

Figure 2: TMS sites were determined by functional localisation and confirmed using frameless stereotaxy (as shown). In each experiment a small figure of 8 coil was used for stimulation of V5 and a standard sized figure of 8 coil was used at the PPC site.

Figure 3:

a: Experiment 1. Search functions and rates for present responses in each task. Both tasks were carried out in a serial manner however the motion/orientation conjunction search was more efficient than the colour/orientation conjunction. Errors shown are \pm SEM.

b: Experiment 2. Differential involvement of right PPC and V5 on colour/orientation conjunction and motion/orientation conjunction search tasks as shown by normalised (with respect to no TMS reaction times) reaction times. Right PPC is significantly impaired in processing of the colour/form conjunction task but not the motion/form conjunction task with rTMS. The opposite pattern is seen with rTMS over V5. Error bars shown are \pm SEM.

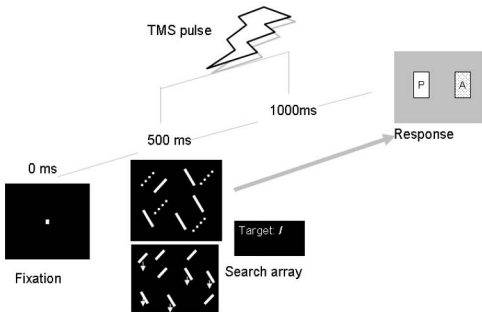
Figure 4: Results of Experiment 3: Normalised effect of the dTMS stimulation over V5 in a motion/orientation task depicted as a function of the post-array onset of the stimulation. Results show that any dTMS stimulation applied more than 100 ms after the onset of the search array produces a significant TMS effect. Errors shown are \pm SEM.

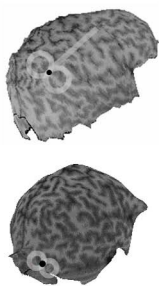
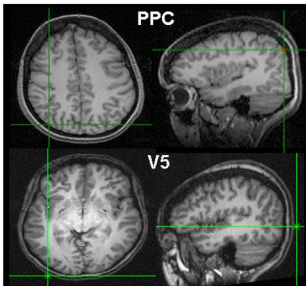
Figure 5: Comparison of normalised TMS effects in motion/orientation task across all four stimulation conditions (for a detailed description of the conditions see Table 1), namely: dTMS over V5 only (collapsed across three time-intervals [100,150,200 ms post-array onset]); dTMS over V5 combined with rTMS over vertex; dTMS over V5 combined with rTMS over PPC; rTMS over PPC only. The TMS effect with the combined stimulation of V5 and PPC was significantly higher than that for all other conditions. Errors shown are \pm SEM.

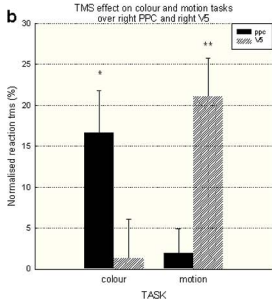
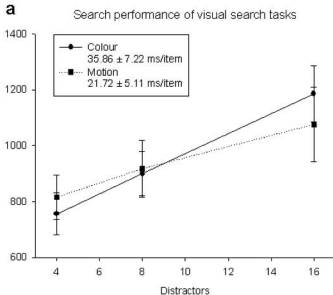
Table 1

TMS effect on reaction time in each hemifield. Figures shown are %TMS effect over non-TMS reaction times \pm standard deviation.

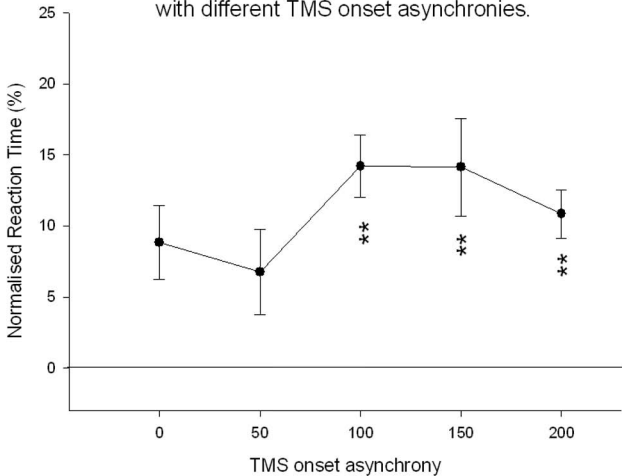
| | LEFT HEMISPACE | RIGHT HEMISPACE |
|--|-------------------|-------------------|
| PPC colour/orientation conjunction | 16.43 ± 10.29 | 17.29 ± 7.98 |
| V5 motion/orientation conjunction | 19.73 ± 11.38 | 21.85 ± 11.10 |
| V5+PPC motion/orientation conjunction | 35.06 ± 16.62 | 37.28 ± 16.08 |
| V5 + vertex motion/orientation conjunction | 11.52 ± 12.46 | 16.32 ± 8.67 |







right V5 normalised TMS effect on the motion conjunction task
with different TMS onset asynchronies.



Normalised TMS effect at four sites.
Moving conjunction task.

